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2019-06

Harlio , A , Kuussaari , M , Heikkinen , R K & Arponen , A 2019 , ' Incorporating landscape heterogeneity into multi-objective spatial planning improves biodiversity conservation of semi-natural grasslands ' , Journal for Nature Conservation , vol. 49 , pp. 37-44 . https://doi.org/10.1016/j.jnc.2019.01

http://hdl.handle.net/10138/302578
https://doi.org/10.1016/j.jnc.2019.01.003

Journal for Nature Conservation 49 (2019) 37–44

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.com/locate/jnc

Incorporating landscape heterogeneity into multi-objective spatial planning improves biodiversity conservation of semi-natural grasslands

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ARTICLE INFO

Keywords:
Agri-environment scheme
Connectivity
Field margin
Landscape heterogeneity
Spatial prioritization
Trade-off

ABSTRACT

Recent actions to mitigate biodiversity loss in agricultural environments appear insufficient despite the considerable efforts channeled via the European Union's Common Agricultural Policy. One likely reason for this failure is the limited attention paid to the regional and landscape level ecological characteristics in farmland conservation planning. We demonstrate how to obtain conservation prioritization solutions that would address simultaneously three goals, including two landscape level targets: minimizing local habitat quality loss, maximizing habitat connectivity, and incorporating landscape heterogeneity. As these goals may be contradictory, we investigate the potential trade-offs between them. We used the Zonation prioritization tool to examine how our three goals could be implemented in the agricultural landscapes of southwest Finland. We used measures of (i) biodiversity value of grasslands, (ii) connectivity between grasslands, and (iii) landscape heterogeneity which comprised of (land cover type based) compositional heterogeneity and (field margin based) configurational heterogeneity. Integration of landscape heterogeneity measures and habitat connectivity resulted in some trade-offs with local habitat quality, the most prominent observation being that landscape heterogeneity co-varied with grassland connectivity. Among the two landscape heterogeneity parameters, inclusion of compositional heterogeneity resulted in more clustered prioritization solutions than configurational heterogeneity, which had a spatially more balanced impact. Concordance among landscape scale factors implies high potential for reconstruction of a functioning network of semi-natural grasslands in areas under intensive agricultural use. Broader scale multi-objective planning approaches can thus importantly support targeting biodiversity conservation planning and mediating the implementation of Common Agricultural Policy objectives.

1. Introduction

Agricultural intensification and associated landscape homogenization has led to widespread biodiversity loss in agricultural environments during the second half of the 20th century (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011; Stoate et al., 2009; Tscharntke, Batáry, & Dormann, 2011). The European Union's Common Agricultural Policy (CAP) has recognized these alarming trends, and thus increasingly supports the implementation of a number of mitigating measures mainly via agri-environment schemes (AES). However, monitoring AES effectiveness since the early 2000s indicates that only half of these measures have caused positive biodiversity effects (Batáry, Dicks, Kleijn, & Sutherland, 2015; Kleijn et al., 2011). One apparent reason for this ineffectiveness is the fact that AES acknowledges poorly the landscape-level effects on biodiversity (Batáry, Báldi, Kleijn, & Tscharntke, 2011; Scheper et al., 2013).

The loss of semi-natural grassland habitats and their connectivity has been drastic during past decades (Cousins, Auffret, Lindgren, & Tränk, 2015; Ekroos et al., 2016; Hodgson, Moilanen, Wintle, & Thomas, 2011; Stoate et al., 2009). This has exposed species inhabiting grassland networks to a number of harmful landscape ecological impacts, such local populations becoming more isolated and vulnerable to extinction, with lowered potential rescue effect (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). This highlights the importance of applying landscape-scale spatial planning to agricultural areas if their biodiversity values are to be maintained.

The establishment of separate conservation areas in a landscape has been the most common biodiversity conservation action, advocated e.g. by the Convention on Biological Diversity (Juffe-Bignoli et al., 2014). Protection and maintenance of semi-natural grasslands has a key role in

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https://doi.org/10.1016/j.jnc.2019.01.003
Received 12 September 2018; Received in revised form 5 December 2018; Accepted 8 January 2019

maintaining biodiversity values in agricultural landscapes, and thus they are often target hotspots for biodiversity conservation efforts in the EU level management planning (Auffret & Cousins, 2011; de Bello, Lavorel, Gerhold, Reier, & Pärtel, 2010; Habel et al., 2013; Hicks, 2010). However, it is challenging to establish large contiguous nature reserves in agricultural landscapes, which are often heavily fragmented and dominated by food production. In addition, leaving land aside for protection does not necessarily fulfil conservation effectiveness in agricultural environments, as e.g. semi-natural grassland habitats generally require active management to preserve their biodiversity values (Dengler, Janišová, Török, & Wellstein, 2014). A complementary approach aiming at the integration of farming practices and conservation actions, may be more readily applied in such landscapes and provide better results for biodiversity conservation as a whole (Ekroos et al., 2016; Fischer et al., 2008; Green, Cornell, Scharlemann, & Balmford, 2005).

It appears increasingly important that the network of protected grasslands should be supplemented by the maintanance and restoration of habitats and structural elements that can support the persistence and movements of grassland species. Indeed, agricultural landscapes often include secondary semi-natural habitats which are not considered in biodiversity conservation. The environmental heterogeneity of agricultural landscapes may have a supportive role for biodiversity and mitigate the negative effects of habitat fragmentation (Rösch, Tscharntke, Scherber, & Batáry, 2013; Tscharntke et al., 2005). It has been argued that protecting scattered solitary parcels of land does not necessarily alone result in successful grassland biodiversity conservation outcomes, as surrounding farmland quality also has an important effect (Dengler et al., 2014; Eycott et al., 2012; Rösch et al., 2013; Slancarova, Benes, Kristynek, Kepka, & Konvicka, 2013; Söderström, Svensson, Vessby, & Glimskär, 2001). However, it should be noted that heterogeneity is a multifaceted issue. Thus, various types of landscape heterogeneity at different spatial scales can have differing biodiversity effects on grassland species (Perović et al., 2015).

AES management actions focus on improving local habitat quality, but they also comprise elements that maintain and add to compositional heterogeneity. During the CAP programme periods 2000–2006 and 2007–2013 the AES system compensated farmers for long-term commitments (5–20 years), providing support for various types of biodiversity, buffer zones and landscape management contracts that all add to the compositional heterogeneity in agricultural environments (Batáry et al., 2015). Organic farming is also one feature of compositional heterogeneity that provides a potential AES-related action to mitigate biodiversity loss (Bengtsson, Ahnström, & Weibull, 2005; Winqvist, Ahnström, & Bengtsson, 2012).

Another type of environmental heterogeneity stems from configurational heterogeneity. Field margins are a significant part of semi-natural areas in agricultural landscapes. They typically make a significant contribution to configurational heterogeneity, and play an important role in maintaining both habitat and species diversity (Marshall & Moonen, 2002). Thus increased field margin edge length can increase diversity, as boundary areas offer specific resources to different species (Concepción, Fernández-González, & Díaz, 2012; Duelli, 1997; Holland et al., 2017; Stoate et al., 2009; Sutcliffe et al., 2015; Sybertz, Matthies, Schaarschmidt, Reich, & von Haaren, 2017).

During past decades spatial conservation planning methods (Appendix 1 in Supplementary data) (Margules & Pressey, 2000) have been developed to assess simultaneously multiple environmental planning problems. Conservation prioritization is inherently a multi-objective problem (Nelson et al., 2009; Pressey, Cabeza, Watts, Cowling, & Wilson, 2007), and trade-offs between different conservation goals are inevitable. Including any additional goal or constraint to an optimization procedure diverges the solution from optimal with respect to the original goal. The multiplicity of goals is emphasized in complex landscapes, such as the agricultural environments described above. Optimization tools have great potential in improving the effectiveness of conservation (Butsic & Kuemmerle, 2015; Margules & Pressey, 2000; Teillard, Doyen, Dross, Jiguet, & Tichit, 2016), since they can simultaneously take into account trade-offs between preservation of priority grassland, habitats and fragmentation of agricultural landscapes.

The key motivation for this study is that neither current nor past AES measures have accounted for habitat connectivity in Finland, or to our knowledge, in any other EU country. This is mainly because, as determined by the CAP, financial aid is allocated at the farm level, based on the voluntary participation of farmers (Arponen et al., 2013). Moreover, it can only be paid to cover the losses of income caused by the implementation of the AES measure which further restricts the use of AES in biodiversity conservation. This is an important shortcoming because habitat fragmentation not only decreases connectivity, but also weakens compositional landscape heterogeneity by reducing the number and size of habitats and increasing unfavourable spatial arrangements of habitats (Brückmann, Krauss, & Steffan-Dewenter, 2010; Perović et al., 2015).

Our study addresses the growing need to integrate the principles of spatial ecology and landscape context to AES targets (Butsic & Kuemmerle, 2015; Ekroos, Olsson, Rundlöf, Wätzold, & Smith, 2014; Whittingham, 2007) because an increase in non-crop habitats is not necessarily an economically and socially feasible solution (Fahrig et al., 2011). We aim to develop an approach and produce results that will provide guidance for improving the effectiveness of AES via spatial planning. With spatial prioritization analyses we aim to answer the following specific questions:

1 How can the spatial arrangement of existing biodiversity-friendly landscape elements supported by AES be included in the conservation prioritization process?
2 How the spatial priorities are changing when local habitat quality, connectivity and landscape heterogeneity are accounted for?
3 What trade-offs (Appendix 1 in Supplementary data) and synergies of biodiversity targets result from a multi-objective conservation planning approach?

2. Methods

We carried out a prioritization analysis using the Zonation software v4.0, which is a framework for spatial conservation prioritization particularly suitable for large grid-based datasets. The Zonation algorithm begins with a complete landscape, and iteratively removes planning units that contribute the least to remaining biodiversity. As a result it produces a complementarity-based hierarchical priority ranking of the units (Moilanen et al., 2005, 2014 and Appendix 1 in Supplementary data).

2.1. Study area

Since AES support is allocated at present at farm level by regional authorities, we chose Southwest Finland (20 000 km^2 in size) as our study area to represent a broader scale European case study area (Fig. 1). Semi-natural grasslands cover ca 2% (39 400 ha) of our study area, of which 27% consists of traditional open semi-natural grasslands (data set 1) and 73% of other types of grasslands (data set 2). The region is the most intensively cultivated part of Finland, with cultivated land covering nearly 25% (Official Statistics of Finland, 2015) of all land area compared to the 5% national average (EEA, 2012). Overall, forests are the most dominant land cover type. The region's agricultural activity is dominated by crop production, animal husbandry being only complementary.

2.2. Data

We used a total of five GIS data sets prepared with ArcGIS (ESRI®

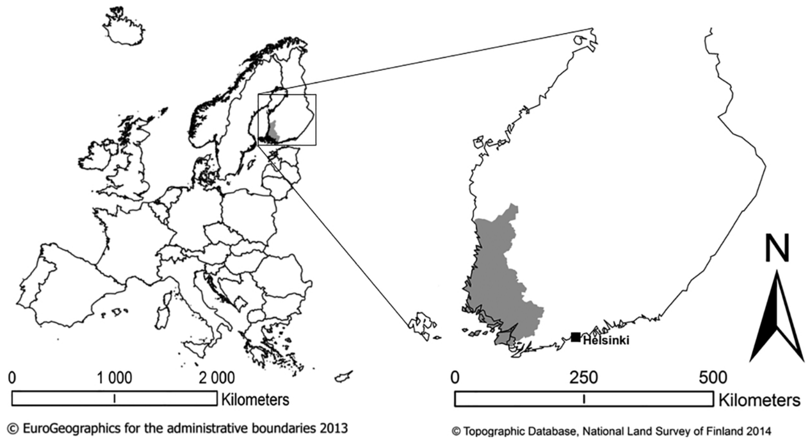

Fig. 1. Study area in Southwest Finland is presented in *grey* on the map.

ArcMAP™ 10.0) for the analyses. We standardized the coordinate systems and transformed the data into 25 m x 25 m resolution raster layers for all raw data sets described in the following sections.

Our primary semi-natural grassland data contained two types of grassland data, which enabled us to define local habitat quality in each grassland raster cell to indicate local-scale conservation value in the prioritization. The data sets (1) and (2) followed the same principles as in Arponen et al. (2013), whereas data sets (3–5) were new and complementary data in the prioritization. The first data set (1) consisted of traditional open semi-natural grassland biotopes classified into nationally, regionally and locally important according to the Finnish national survey of valuable grasslands (Vainio, Kekäläinen, Alanen, & Pykälä, 2001). The second data set (2) consisted of all other grasslands not included in the Finnish national survey, derived from the SLICES land cover database provided by Statistics Finland 2005 database, and including locally valuable sites such as long-term set-asides (National Land Survey of Finland). Each EU member state is obliged to annually collect its own Integrated Administration and Control System (IACS) database (Lomba et al., 2017), which provides land-use information for AES in spatial format. The third data set (3) consisted of the Finnish IACS data on semi-natural grasslands under management contract and receiving agri-environment payments via AES received from Statistical Services, Ministry of Agriculture and Forestry 2007 database (Table 1 and Fig. 2, A).

Our secondary semi-natural grassland data consisted of landscape heterogeneity elements that we partitioned into (land cover type -based) compositional heterogeneity for the fourth data set (4), and (field margin -based) configurational heterogeneity for the fifth data set (5).

To assess compositional heterogeneity in the analysis, we compiled various landscape elements that are known to provide habitat variability or resources to grassland species. For this, we further explored the third data set (3) of the Finnish IACS data concerning field parcels (Statistical Services, Ministry of Agriculture and Forestry 2007). These data included the land-use information for each field parcel in the landscape. (Table 1 and Fig. 2, B and Appendix 1 in Supplementary data).

As a measure of configurational heterogeneity, we included the edge density of field margins into the analyses utilizing the field parcel boundaries of the third data set from the Finnish IACS. Increased edge density refers to more heterogeneous and mosaic-like landscape configuration, as the number, size and arrangement of certain habitat types increase. In addition, we separated different types of field margins (data sets (4) and (5)) because their influence on grassland biodiversity differs (see Appendix 1 in Supplementary data). In the next step, we normalized the values to the same relative weight with compositional heterogeneity data (Table 1 and Fig. 2, C).

Table 1
Raster layers created for the analyses and their relative weights used in Zonation prioritization. Values for configurational heterogeneity feature data were normalized to the same relative weight with compositional heterogeneity feature data. Justification for weight setting is provided in the Appendix 1 in Supplementary data.

BIODIVERSITY FEATURE LAYER	WEIGHT	DATA SET
Prioritized grassland feature data		
Nationally valuable semi-natural grasslands	40	1
Regionally valuable semi-natural grasslands	30	1
Locally valuable semi-natural grasslands	20	1
Uncategorized grasslands with semi-natural grassland management contract[a]	20	3
Uncategorized grasslands	10	2
Landscape heterogeneity feature data		
Compositional		
Semi-natural grassland management contract[a]	20	3
Biodiversity contract 20 years[a]	16	3
Biodiversity contract 10 years[a]	14	3
Biodiversity contract 5 years[a]	12	3
Permanent pastures[a]	12	3
Buffer zone contract 20 years[a]	10	3
Buffer zone contract 10 years[a]	8	3
Animal husbandry farms	8	3
Buffer zone contract 5 years[a]	6	3
Organic farming[a]	4	3
Dairy cattle farms	4	3
Configurational		
Edge density of field-field margins	0–20	3
Edge density of field-forest margins (values doubled)	0–20	4
Edge density of field-waterway margins	0–20	5

[a] These features belong to the agri-environment scheme (AES) support system in EU's Common Agricultural Policy during the programme period 2007–2013.

2.3. Conservation priority settings for Zonation

Zonation allows users to determine the relative importance of each feature layer by setting weights, which influences the emerging prioritization solutions (Moilanen et al., 2011). We applied the following principles in the feature weighting that was carried out in ArcGIS (Table 1 and Fig. 2): weights for classified semi-natural grassland data (data set (1)) were assigned according to the conservation value set by the Finnish national survey, and following Arponen et al. (2013). Weights for the second data set, which was uncategorized and included all types of treeless grasslands, were given the lowest value. This was due to limited knowledge of their exact conservation value, but their potential as suitable habitat for common grassland species, along with their locations for future restoration actions.

Weights for the landscape heterogeneity data (third to fifth data

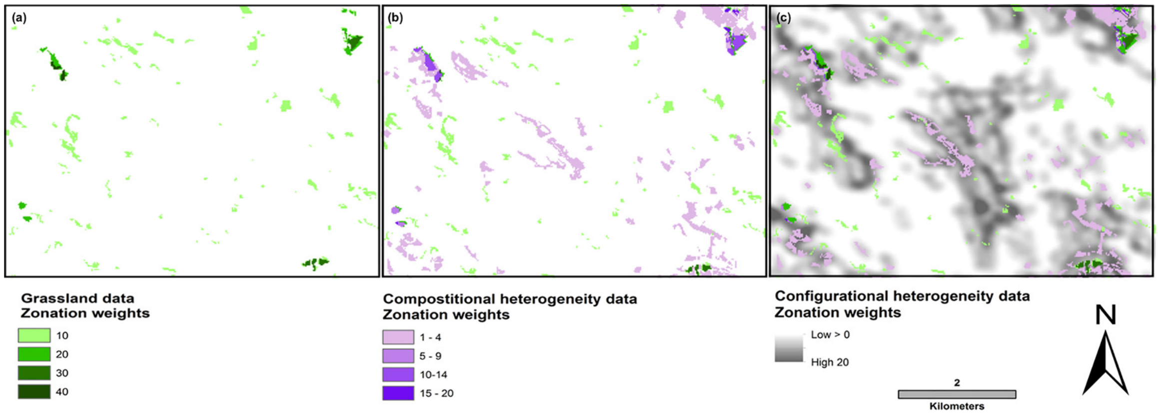

Fig. 2. An example of geographical positioning of grassland data and landscape heterogeneity elements in our data. (a) Grassland habitats are small in size and fragmented around the landscape in our data. (b) Compositional i.e. land cover type based heterogeneity data in the same landscape. They partially overlap with data in (a) because some grasslands are under AES program. (c) Configurational heterogeneity data i.e. field margin areas in the same landscape. Elements are blurry because the effect of field margin (sphere of influence set to 200 m) diminishes smoothly with increasing distance from the margin center and overlaying margin areas receive higher values (Kernel density effect).

sets) were assigned according to their relative importance to grassland biodiversity based on scientific literature (explained in more detail in Appendix 1 in Supplementary data).

2.4. Connectivity settings for Zonation

Both patch quality and habitat connectivity need to be examined while assessing the functionality of a habitat network from the perspective of metapopulation dynamics (Schooley & Branch, 2011). Grassland-to-grassland connectivity was set to correspond to a mean dispersal of two km, which is an appropriate scale for many mobile grassland species (Moilanen & Nieminen, 2002). This distance indicates the mean of the negative exponent dispersal kernel used in the “Distribution smoothing” in Zonation, meaning that ca. 63% of the dispersal events would be shorter than 2 km, with shortest distances having the highest weight. Smoothing spreads out the value of the focal cell into its surroundings, i.e. whenever many cells occur nearby, the overlapping kernels ensure that the larger the site and the shorter the distances to other sites are, the higher the value in the prioritization. Hence, species with more strict connectivity requirements also benefit from this, even though the solution is optimized for the 2 km mean dispersal.

In addition to connectivity between grassland sites, we considered the proximity of grassland sites to elements in the heterogeneity layers via the “Ecological Interactions” option in Zonation. This means that the heterogeneity elements were not prioritized themselves, but they influenced the prioritization ranking value of the grassland sites based on how far the elements were situated from the grassland site under consideration. The scale for this influence was also set to two km. This means that, when other prioritization elements are equal, a grassland site falling within the two-km connectivity kernel around a heterogeneity element will receive a higher heterogeneity value and thus rank higher in the Zonation prioritization than a grassland falling outside the two-km connectivity kernels. Thus, the influences of connectivity and landscape heterogeneity on grassland prioritization were set at an equal level.

2.5. Zonation functions for landscape analyses

First, we applied the option of transformed layers output -function in Zonation. It calculates connectivity transformations onto all input biodiversity feature layers (Table 1) prior to the actual ranking process, and this function produces output maps of these transformed input layers (Moilanen et al., 2014). It simultaneously considers size, form, arrangement and weight of the landscape heterogeneity data in relation to the grassland data. The transformed layers allowed us to directly and separately view the effects of the compositional and configurational landscape heterogeneity elements, and connectivity of the grassland parcels prior to Zonation ranking. This examination allowed us to detect spatial patterns and correlations among the various factors.

Second, we carried out two sets of actual Zonation prioritization analyses: (1) “Basic” analysis, which included the prioritization of conservation value on grassland data only and (2) “Landscape” analysis where we added landscape heterogeneity elements into the prioritization. We replicated both analyses with grassland-to-grassland connectivity, resulting in a total of four priority rank maps. The grassland data (data sets 1, 2 and partially 3; see Table 1) were the only data that were ranked in the Zonation prioritization. In contrast, the heterogeneity data were not ranked, but used indirectly to drive the priorities towards more heterogeneous landscapes.

We used the Additive benefit function -variant of Zonation, which takes into account all weighted features in a cell instead of only the highest feature value, i.e. all biodiversity features (Table 1 and Fig. 2) in a given cell are summed. This function variant is considered most appropriate when the features are essentially surrogates for species such as the habitat types in our study.

2.6. Post-processing of results

We calculated correlations between the three transformed output layers (i.e. habitat connectivity and compositional and configurational heterogeneity). The correlations and significance values were obtained with the Raster package in R v3.2.1 (R Development Core Team, 2008). Correlation coefficients depict the relationship between two raster layers, which is a measure of dependency between the layers. A positive correlation indicates a direct relationship between two layers, whereas a negative correlation means that one variable changes inversely to the other.

Hierarchical priority rankings produced in the analysis were customized into selected top fractions for cartographical use and charts in ArcGIS and R. These categorizations visualized the differences between each analysis variant.

3. Results

The application of transformed output layers prior to the actual prioritization showed that landscape elements improving ecological quality and compositional heterogeneity coincide with high grassland connectivity. A very strong positive correlation was observed between grassland site connectivity and (land cover type -based) compositional landscape heterogeneity, whereas correlations were lower for the other

Table 2
Pearson's correlation coefficients of transformed input layers produced by Zonation prior to the actual prioritization ranking process. Highest positive correlation (0.92) indicates that better-connected grassland sites are located in landscapes with higher (land cover type based) compositional heterogeneity than (field margin based) configurational heterogeneity.

	Correlation coefficients Compositional hetetogeneity	Configurational heterogeneity	Connectivity
Compositional heterogeneity	1	0.71*	0.92*
Configurational heterogeneity	0.71*	1	0.62*
Connectivity	0.92*	0.62*	1

* $p < 0.01$.

pair-wise comparisons (Table 2). Note that all correlations are high because they result from the transformations made on the same raw data layers, and thus it is necessary to focus on the relative differences between different pairwise comparisons rather than absolute values. This result indicates that valuable, well-connected grasslands tend to cluster especially in landscapes where landscape elements beneficial to biodiversity are more abundant.

Our multi-objective prioritization analyses were simultaneously able to account for local habitat quality, landscape heterogeneity and connectivity. Broader-scale biodiversity targets (i.e. connectivity and landscape heterogeneity) resulted in solutions where local habitat quality targets were compromised and not fully optimal (Fig. 3). When these trade-offs occurred, some of the most valuable semi-natural grasslands based on local habitat quality were lost from the topmost 10% conservation priority fraction due to poor connectivity and low landscape heterogeneity (Fig. 3).

We also detected various grades of trade-offs between different landscape-level objectives. Local habitat quality was compromised very slightly when only landscape heterogeneity (both compositional and configurational) (Fig. 3, b) was included in the prioritization, whereas connectivity (Fig. 3, c) resulted in greater trade-offs in the top 10% fractions. Including both connectivity and landscape heterogeneity into prioritization resulted in the largest, synergistic impact on the trade-off effect (Fig. 3). Moreover, certain sites were valuable based on their local habitat quality, but which concurrently were both isolated and occurred in landscapes that were not particularly heterogeneous.

4. Discussion and conclusions

We included valuable grassland habitats, biodiversity-rich landscape elements and compositional and configurational heterogeneity aspects together with their connectivity into our multi-objective landscape-scale spatial conservation prioritization. These aspects determine many key ecological processes, which influence biodiversity in agricultural environments.

The key finding emerging from our prioritization results is that

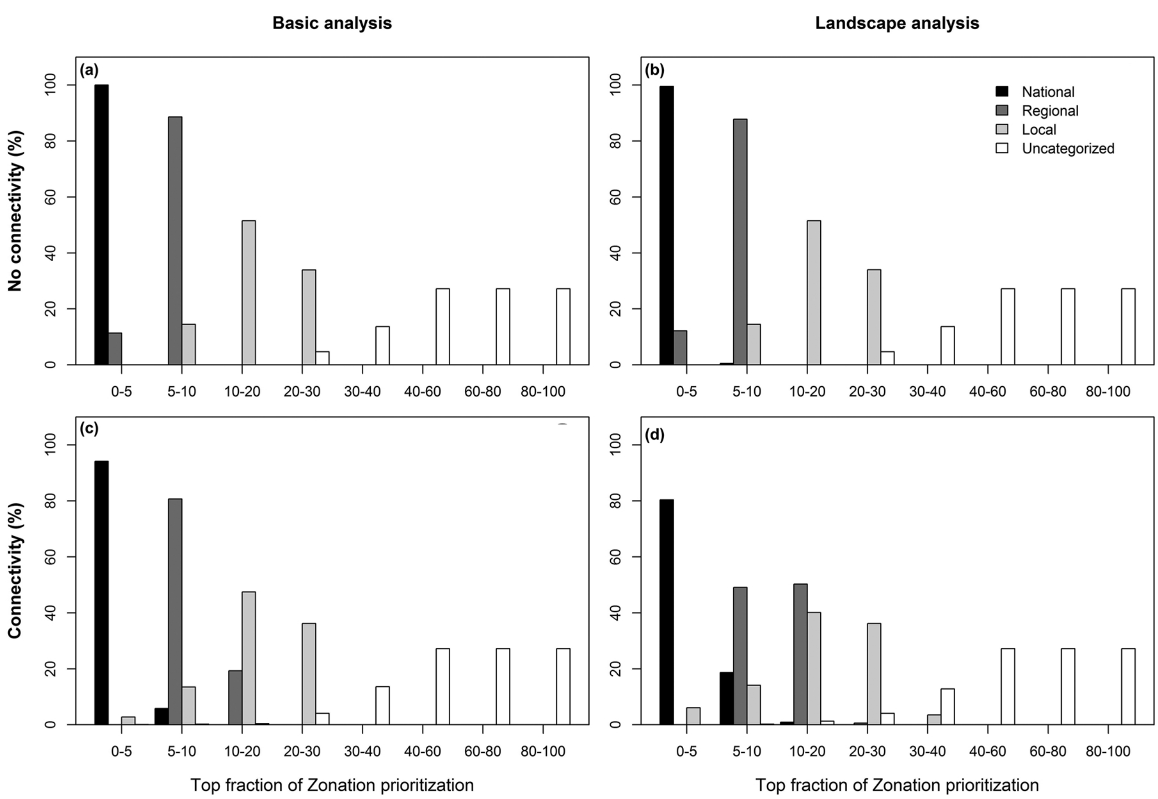

Fig. 3. Division of grassland data in Zonation prioritization ranking into different top fractions in" Basic" and" Landscape" analyses with and without connectivity. X-axis shows how the prioritized grassland data falls into different top fractions and y-axis shows the percentage of each grassland category left in different top fractions, e.g., in panel (d) the top 5% fraction of cells contains 80% of all nationally valuable semi-natural grasslands. Changes in top fraction of different analysis variants illustrate the trade-offs for local habitat quality. The greatest loss of most valuable semi-natural grasslands from the top priority fraction can be found when both landscape heterogeneity and connectivity are integrated in landscape level prioritization (d compared to a). Landscape heterogeneity alone does not result in a trade-off with local habitat quality (b compared to a). Connectivity alone results in modest trade-offs with local habitat quality (c compared to a).

landscape elements that improve ecological quality and compositional heterogeneity coincide with high grassland connectivity. This result has a number of implications for the targeting of AES support to the management of semi-natural grasslands, and to the identification of candidate sites for habitat restoration. Such synergies highlight the importance of tackling AES allocation as a landscape-level or regional interconnected process instead of considering the management of each semi-natural grassland site in a given region separately from the others.

Because of a drastic decrease in the amount of semi-natural grassland habitats in past decades the protection of these habitats has been seen as the primary conservation objective (Ekroos et al., 2016; Hodgson et al., 2011; Prevedello & Vieira, 2010; Török, Hölzel, Diggelen van, & Tischew, 2016). In our conservation prioritization we emphasized the importance of high-quality semi-natural grassland habitat over habitat quantity because other grassland habitats included in our study landscape are unlikely to provide additional high-quality habitats for threatened and declined grassland species. This is supported by Ekroos et al. (2016), who emphasize that traditional semi-natural grasslands usually have a long management history that has generated distinctive animal and plant species compositions (and, for example, associated seed banks) that cannot easily be substituted by other younger grasslands.

However, the amount of high-quality habitat is so low that they alone cannot halt the decline of grassland species. Our approach is especially useful for identifying high-quality landscape areas where restoration efforts should be concentrated. These sites may support present as well as re-established farmland biodiversity by enhancing connectivity and the probability of dispersal between high-quality sites (Raatikainen, Mussaari, Raatikainen, & Halme, 2017). In other words, although grassland patches with lower habitat quality do not necessarily provide suitable sites for the long-term population regeneration and persistence, for example for grassland butterfly species, they can support the movements between key habitat patches by providing nectar sources and sheltered resting sites (Ockinger & Smith, 2008; Villemey et al., 2015). More generally, as illustrated by our analysis, inclusion of grassland sites with lower local quality in broader-scale prioritization can enhance the consideration of multi-objective landscape-level ecological processes.

In many areas the decrease in semi-natural grassland habitats has led to habitat fragmentation, which decreases connectivity and compositional landscape heterogeneity by reducing the number and size of habitats and increases their unfavourable arrangement (Brückmann et al., 2010; Perović et al., 2015). Effective semi-natural grassland biodiversity conservation outcomes cannot therefore be achieved only through protecting land, but acknowledging the significance of the surrounding farmland matrix quality is essential (Eycott et al., 2012; Janišová, Michalcová, Bacaro, & Ghisla, 2014; Rösch et al., 2013; Slancarova et al., 2013; Söderström et al., 2001). These arguments were supported by our conservation prioritization results that showed trade-offs of isolated high-quality patches in less heterogeneous landscapes, indicating that sparing habitat quantity and quality alone does not lead to optimal conservation outcomes. However, it should be noted that even small habitat fragments can maintain overall biodiversity when their spatial arrangement is favorable, i.e. when they are well-connected (Tscharntke, Steffan-Dewenter, Kruess, & Thies, 2002; Tscharntke et al., 2012).

In order to produce a wholesale assessment of the relative importance of isolated high-quality patches vs. ecological connectivity and matrix heterogeneity, one would need very detailed information on where species of conservation concern currently occur, what are their dispersal abilities and what the potential of species' local populations showing an extinction debt is. However, such data are rarely available for areas as large as our study area. In the absence of such data we must rely on general assumptions based on past research for the analyses. Due to this uncertainty and to the extremely small number of high quality grasslands within our study area, trading off isolated high quality sites for well-connected poor quality sites in practice should be conducted only with extreme caution. Rather, the priorities could be used to identify places worthy of further conservation and restoration investments, in addition to the currently managed sites.

The secondary landscape elements generate a more heterogeneous landscape where many habitat generalists may profit from secondary patches as complementary resources and movement facilitators (Tscharntke et al., 2012). In our conservation prioritization, areas with higher compositional heterogeneity also support higher connectivity. This may reflect historical land use of this specific landscape, where increasing crop production intensity has had agglomerating biodiversity degradation effects. According to our prioritization analysis, relatively high configurational heterogeneity was occasionally preserved even in otherwise homogeneous and intensively farmed areas in the form of dense field margin networks. The question whether the coincidence of well-connected grassland habitats and compositional heterogeneity is a common characteristic of agricultural landscapes remains open to debate. If there is, as a rule, such a positive relationship, it would simplify the conservation prioritization for directing the landscape features of AES (Table 2) to better support biodiversity conservation of high-quality semi-natural grassland habitats. This expectation is in line with the results of Ekroos et al. (2016), which indicated that devoting specific areas of non-crop habitats to conservation outside intensive crop production could lead to more effective biodiversity conservation.

The existing EU Common Agricultural Policy contains financial support for management actions for both primary and secondary semi-natural grassland habitat as an incentive for farmers to adopt biodiversity-friendly farming practices. Our Zonation-based demonstration illustrates how the spatial arrangement of an equivalent area may vary between differently weighted conservation prioritizations. This implies high flexibility and potential for the reconstruction of a functioning network of semi-natural grasslands even in areas under intensive agricultural use. Moreover, our conservation prioritization enables the identification of those area networks that would benefit from targeted AES measures.

In the light of our results, the effectiveness of AES for biodiversity conservation might be improved without additional financial inputs, if management actions would be regionally better coordinated, and readily available and adopted by farmers. To support the successful conversion of spatial plans into practice via such voluntary-based conservation measures, farmers need to be encouraged in different ways to participate. This could include e.g. (1) targeted marketing of AES activities to farmers with potential high-quality sites, (2) agglomeration bonuses for active farmers or (3) higher compensation for maintenance of higher-quality sites. This kind of improved planning could result in spatially cohesive, high-quality habitat networks with landscape-ecological characteristics that facilitate maintenance or restoration of biodiversity. It would also support institutional development and participation of stakeholders in complex social-ecological farming systems as recommended by Hodge, Hauck, and Bonn (2015) and improve targeting, monitoring and evaluating biodiversity actions (Lomba et al., 2017). We believe that multi-objective optimization considering both grassland conservation and landscape element aspects can help with targeting biodiversity conservation more effectively in situations with socio-economical pressure caused by demand for food production and agricultural industry and can help mediate the implementation of CAP objectives.

Declaration of interests

None.

Acknowledgements

A.H. was supported by a grant from the Kone Foundation (application number 46-6446). Aija Kukkala and Ninni Mikkonen made valuable comments on earlier versions and helped to improve the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.jnc.2019.01.003.

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